

End-to-end foodweb control of fish production on Georges Bank

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The ecosystem approach to management requires the productivity of individual fish stocks to be considered in the context of the entire ecosystem. We derive an annual end-to-end budget for the Georges Bank ecosystem, based on data from the GLOBEC programme and fisheries surveys for the years 1993–2002. Scenarios based on this budget describe the consequences of various alterations in the Georges Bank trophic web: reduced nutrient input, increased benthic production, removal of carnivorous plankton, and changes in species dominance within fish guilds. Potential yields of cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) are compared with historical catches and estimates of maximum sustainable yield (MSY) from recent stock assessments. The MSYs of cod and haddock can be met if the fish community is restructured to make them the dominant species in their respective diet-defined guilds. A return to the balance of fish species present in the early 20th century would depend on an increase in the fraction of primary production going to the benthos rather than to plankton. Estimates of energy flux through the Georges Bank trophic web indicate that rebuilding the principal groundfish species to their MSY levels requires restructuring of the fish community and repartitioning of energy within the foodweb.

Keywords: community dynamics, ecosystem-based management, end-to-end, Georges Bank, marine fish.

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Introduction

The super-abundance of cod (*Gadus morhua*) on the fishing grounds of the Northwest Atlantic fuelled the development of early settlements in North America (Kurlansky, 1997; Rosenberg *et al.*, 2005). The collapse of cod and other principal groundfish stocks was caused primarily by excessive fishing mortality, but the delayed recovery of some stocks has been attributed to several factors in addition to overfishing. Climate change (Beaugrand *et al.*, 2003), regime shifts (Choi *et al.*, 2004), trophic cascades (Frank *et al.*, 2005), and habitat disturbance (National Research Council, 2002) have all been invoked as causes of ecosystem change, and the proliferation of pelagic fish (Frank *et al.*, 2005), elasmobranchs (Myers *et al.*, 2007), jellyfish (Jackson *et al.*, 2001), and crustaceans (Worm and Myers, 2003) are described as consequences. These explanations are based predominantly on correlations between individual species or trophic groups and do not quantify the changes in energy fluxes within the overall foodweb.

Measures to halt overfishing and to rebuild depleted groundfish stocks (effort reduction, gear modification, and area closures) were implemented by the New England Fishery Management Council from 1993 and are continuing with subsequent amendments to the fishery management plans (Fogarty and Murawski, 1998). The US Sustainable Fisheries Act mandates rebuilding of overfished stocks to levels capable of achieving maximum sustainable yield (MSY) within 10 years (Safina *et al.*, 2005). MSY estimates

are uncertain, not only because they require knowledge of the productivity and compensatory capacity of each stock, but also because they often imply rebuilding to levels beyond those observed in recent decades. Further, it is difficult to derive quantitative estimates of the abundance of the pristine stocks, either from historical data (Rosenberg *et al.*, 2005) or by solving for the unfished biomass from population models (Myers *et al.*, 2001). As fish stocks begin to rebuild, there is some doubt whether MSY levels of individual stocks can be attained collectively, given increases in non-commercial species (Link, 2007) and other changes in the marine ecosystem. Decreased growth rates, particularly in haddock (*Melanogrammus aeglefinus*; NEFSC, 2008), can be interpreted as density-dependent growth caused by limited food supply.

A new assessment of the Georges Bank ecosystem (Figure 1) provides estimates of production at all trophic levels (Steele *et al.*, 2007). We use a unified version of this web to calculate the effects on all trophic groups of a range of adjustments to the internal structure of the ecosystem. These different scenarios determine the consequent changes in the production of three fish guilds, planktivores, benthivores, and piscivores (Figure 1). We estimate the potential production of cod, a piscivore, and haddock, a benthivore, under different foodweb scenarios, using the maximum fraction that the individual species contribute to the trophic guilds. We compare these scenarios with observed patterns of yields of cod and haddock during the 20th century. Finally, we evaluate the extent to

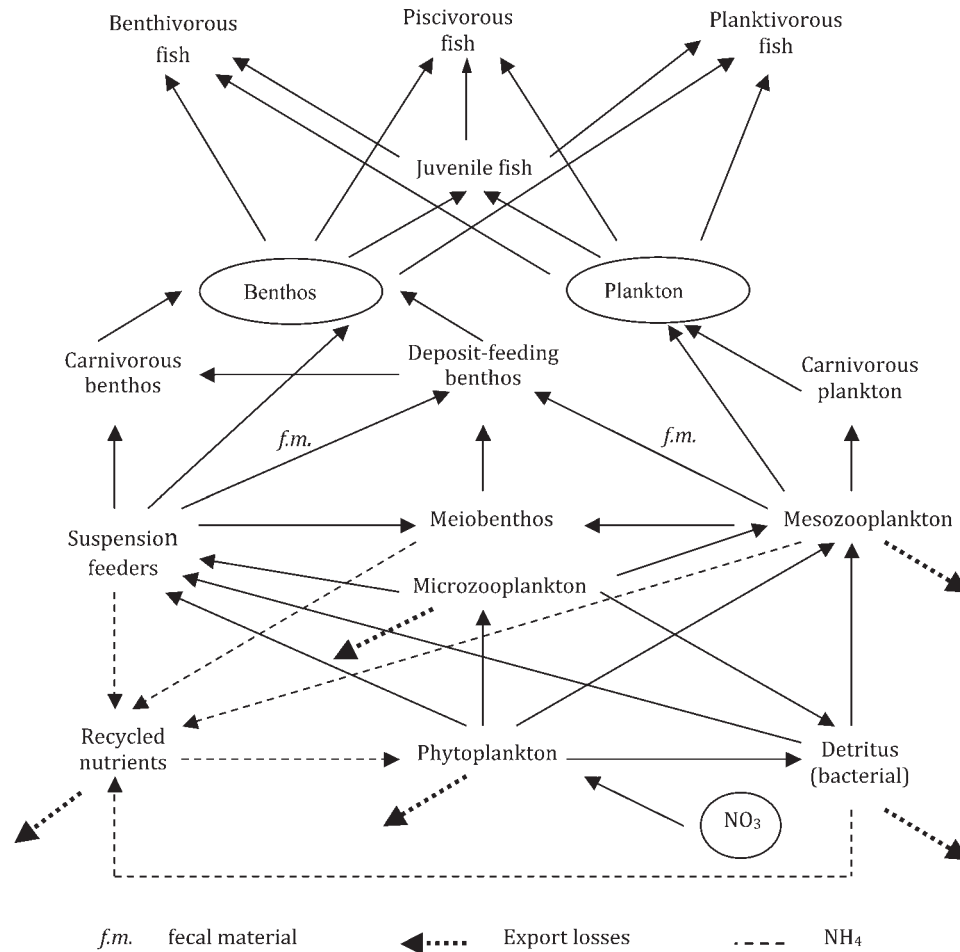


Figure 1. Georges Bank foodweb. Solid arrows represent predator–prey links. The input, NO_3 , drives the microbial foodweb including recycling of nitrogen as NH_4 (dashed lines). Dotted lines are physical losses. The ovals for Plankton and Benthos indicate the food available for the fish guilds. See Table 3 for the flux values.

which rebuilding the cod and haddock stocks to MSY levels is constrained by the basic productivity of the ecosystem.

Foodweb analysis

A general equation for a prey–predator foodweb (Steele, 2009) is

$$\frac{dB_i}{dt} = e_i \left(\sum_j Q_{ij} + G_i \right) - \sum_i Q_{ij} - L_i, \quad (1)$$

where B_i is the biomass of “trophic component” i , Q_{ij} the rate at which B_j is consumed by B_i , G_i the gains from external sources, and L_i the losses from the system, with G_i and $L_i > 0$. The transfer efficiency, e_i , calculated as production (P_i)/consumption (C_i), is assumed constant for each component i .

The units of biomass can be energy, live weight, particulate organic carbon, or a nutrient such as nitrogen. In the last case, consumption can include nutrients recycled from heterotrophs to autotrophs. This is the most general formulation, with Q_{ij} as variables. As there are typically many more Q_{ij} than equations, the usual practice is to associate a single variable with each compartment—biomass, production, or consumption rate—and to linearize the system, permitting matrix solutions for the

steady state. There are two options:

$$(A) \quad Q_{ij} = a_{ij}P_j \quad a_{ij} \geq 0 \quad (\text{bottom-up})$$

and

$$(B) \quad Q_{ij} = b_{ji}C_i \quad b_{ji} \geq 0 \quad (\text{top-down}).$$

Option (A) follows the expected direction of energy flux, with production by prey determining the intake by predators (Steele, 1974; Sissenwine *et al.*, 1984). In option (B), consumption by the predator determines the output from the prey (Christensen and Pauly, 1993). Therefore (A) describes bottom-up control, and (B) describes top-down control.

Application to Georges Bank

Recently, the desire to construct end-to-end budgets that encompass external forcing from both climate change and fishing has led to combinations of the two approaches (Aydin *et al.*, 2005; Field *et al.*, 2006; Plagányi, 2007), with bottom-up depictions forced by nutrient fluxes into the system (e.g. NEMURO; Fuji *et al.*, 2002), and top-down treatments starting from fisheries yields (e.g. ECPATH; Christensen and Pauly,

1993). Steele *et al.* (2007) followed this general approach, dividing the ecosystem components into lower and upper trophic webs because of their disparate space-/time-scales and different relation to physical processes (Steele and Collie, 2005). The lower foodweb is driven by nutrient recycling and by physical influx of NO_3 -rich deeper water, with concomitant export off Georges Bank of near-surface water and associated plankton. To encompass the spatial and temporal variability, Steele *et al.* (2007) constructed nine budgets for three seasons in three distinct hydrographic regimes on Georges Bank. The output from the nine budgets was used to estimate the annual average fluxes from the lower to the upper components of the web. The data on NO_3 fluxes to drive this part of the system, and the data on plankton and benthos to constrain the output, were derived largely from GLOBEC surveys from 1995 to 1999 (Wiebe *et al.*, 2001). The output is expressed as annual average production ($\text{gC m}^{-2} \text{ year}^{-1}$) of meso-zooplankton, and suspension- and deposit-feeding macrobenthos (Figure 1).

Fish biomass data from trawl surveys on Georges Bank from 1963 to 2002 (Smith, 2004; Steele *et al.*, 2007) were partitioned into piscivores, planktivores, and benthivores (Table 1) based on fish diets (Garrison and Link, 2000). For the budget calculations, we used the decade 1993–2002, which coincides with the period of the Georges Bank GLOBEC field programme. Further, we assumed that (i) the fish eaten by other fish are juvenile prerecruits (Overholtz *et al.*, 2000) that eat predominantly zooplankton, and

(ii) this piscivory is the dominant source of mortality of the prerecruits. These data and our assumptions permitted us to make top-down estimates of the food requirements of the fish communities on Georges Bank in terms of two functional, rather than species, groups: total plankton and total benthos (Figure 1). The top-down and bottom-up fluxes were matched for the decade 1993–2002 by estimating the required fluxes through the invertebrate carnivore components of the plankton and benthos (Figure 1), then comparing these fluxes with the available observations (Steele *et al.*, 2007). Flux estimates for these components of the foodweb generally have relatively large uncertainties, so are often used to reconcile web budgets (Mackinson and Daskalov, 2007; Link *et al.*, 2008).

The main findings of previous work

Three patterns of variability in the Georges Bank ecosystem, which are influenced by some combination of climatic change and fishing pressure, are relevant to this analysis.

- (i) The 40 years of data for fish populations revealed great interannual and interdecadal variation in species composition (Steele *et al.*, 2007; Gifford *et al.*, 2009) and in the three feeding guilds (Figure 2a). Over time the species composition shifted from benthivores in the first decade to piscivores in the third decade and to planktivores in the second and last decades (Figure 2a). The species in each trophic guild actually feed to different degrees on all three prey categories (Table 1). Benthivores (e.g. haddock and ocean pout, *Macrozoarces americanus*) and planktivores (e.g. herring, *Clupea harengus*, and mackerel, *Scomber scombrus*) are more restricted in their diets, but piscivores (e.g. cod and winter skate, *Leucoraja ocellata*) have an average intake spread fairly evenly among plankton, benthos, and juvenile fish. The piscivores should in fact be termed omnivores, but we retain the conventional nomenclature to emphasize

Table 1. Percentage diets of the three fish guilds.

Guild	Benthos	Plankton	Fish
Benthivores	85 (82–88)	11 (8–14)	4 (0–10)
Planktivores	14 (3–25)	82 (74–91)	4 (0–10)
Piscivores	42 (37–45)	24 (18–29)	34 (28–37)

Average and range for the four decades 1963–2002 (after Garrison and Link, 2000).

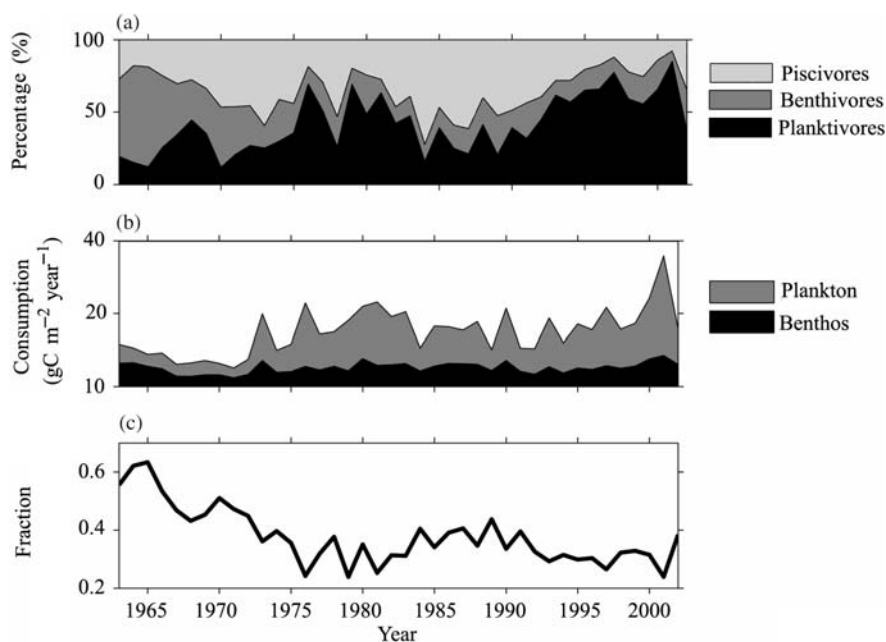


Figure 2. Time-series of (a) percentage biomass in the three fish guilds, (b) consumption of benthos and plankton by the fish community, and (c) fraction of benthos in the total food intake of plankton plus benthos.

Table 2. The production matrix, $AP = [a_{ij}]$ for an end-to-end Georges Bank foodweb, expressed as the percentage of nitrogen or carbon transferred from foodweb component j (columns) to component i (rows) including recycling in the lower web—note that in the actual calculations [Equation (3)], the a_{ij} are proportions.

B1	B2	B3	B4	B5	B6	B7	B8	B9	B10	B11	B12	B13	B14	B15	B16	B17	
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	B1 Inorganic N
100	0	0	0	0	100	0	0	0	100	0	0	0	0	0	0	0	B2 Phytoplankton
0	60	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	B3 Microzooplankton
0	26	21	0	0	0	0	0	0	0	14	0	0	0	0	0	0	B4 Mesozooplankton
0	0	0	14	0	0	0	0	0	0	0	0	0	0	0	0	0	B5 Inv. carn. plankton
0	6	3	0	0	0	0	0	0	0	3	0	0	0	0	0	0	B6 Susp. feed benthos
0	0	0	4	0	4	0	0	0	0	0	0	0	0	0	0	0	B7 Meiobenthos
0	0	0	16	0	16	100	0	0	0	0	0	0	0	0	0	0	B8 Dep. feed benthos
0	0	0	0	0	10	0	54	0	0	0	0	0	0	0	0	0	B9 Inv. carn. benthos
0	0	53	56	0	60	0	0	0	0	83	0	0	0	0	0	0	B10 Bact. recycling
0	8	23	0	0	0	0	0	0	0	0	0	0	0	0	0	0	B11 Detritus
0	0	0	9	100	0	0	0	0	0	0	0	0	0	0	0	0	B12 Plankton for fish
0	0	0	0	0	10	0	46	100	0	0	0	0	0	0	0	0	B13 Benthos for fish
0	0	0	0	0	0	0	0	0	0	0	39	29	0	0	0	0	B14 Juvenile fish
0	0	0	0	0	0	0	0	0	0	0	54	26	47	0	0	0	B15 Planktivores
0	0	0	0	0	0	0	0	0	0	0	1	28	10	0	0	0	B16 Benthivores
0	0	0	0	0	0	0	0	0	0	0	6	17	43	0	0	0	B17 Piscivores

Table 3. Annual values of nutrient input (G), transfer efficiency (e), and fractional physical loss (f) for Equation (3), and the resultant rate of annual production P .

Foodweb component	G	e	f	P
B1 NO_3	127.0	1.00	0	127.0
B2 Phytoplankton	0	1.00	0.0493	344.0
B3 Microzooplankton	0	1.00	0.0346	201.4
B4 Mesozooplankton	0	1.00	0.1849	118.6
B5 Invertebrate carnivorous plankton	0	0.20	0	3.33
B6 Suspension-feeding benthos	0	1.00	0	26.21
B7 Meiobenthos	0	0.20	0	1.17
B8 Deposit-feeding benthos	0	0.20	0	4.88
B9 Inv. carn. benthos	0	0.20	0	1.07
B10 Bact. recycling	0	1.00	0.0426	233.9
B11 Detritus	0	1.00	0.1567	63.69
B12 Plankton for fish	0	1.00	0	13.59
B13 Benthos for fish	0	1.00	0	5.857
B14 Juvenile fish	0	0.30	0	2.110
B15 Planktivores	0	0.10	0	0.988
B16 Benthivores	0	0.10	0	0.200
B17 Piscivores	0	0.10	0	0.264

G and P are in units of $\text{g C m}^{-2} \text{ year}^{-1}$.

predation on fish in the foodweb. Partitioning of consumption among guilds will be altered by changes in the lower trophic web.

- (ii) Fish consumption of plankton plus benthos (Figure 2b) showed a marked increase in total food intake by fish after the first decade of the time-series. Steele *et al.* (2007) attributed the markedly lower consumption during the years 1963–1972 to less primary production resulting from a significantly decreased concentration of NO_3 (Petrie and Yeats, 2000) in an intrusion of the cold Labrador Current (Pershing *et al.*, 2001) at the shelf edge. Because the foodweb model assumes linear responses, reductions in primary production are distributed proportionally among the three trophic groups.

- (iii) There was a marked decrease in benthos as a fraction of total food consumption by fish (Figure 2c). Steele *et al.* (2007) attributed this to a decrease in the epifaunal suspension feeders that compete for phytoplankton (Figure 1), possibly through habitat destruction (National Research Council, 2002; Hermesen *et al.*, 2003).

Bottom-up representation of the end-to-end foodweb

Here, we have converted the top-down and bottom-up components to a single bottom-up representation of the annual average production by each element of the total foodweb in carbon units. For the fish components, we took averages for the decade 1993–2002, which corresponds most closely to the GLOBEC years used for the lower web calculations. For the lower web, we took weighted averages over the spatial domains and seasons.

From Equation (1) the resultant expression for a bottom-up foodweb at steady state is

$$e_i \left(\sum_j a_{ij} P_j + G_i \right) - \sum_j a_{ji} P_i - f_i P_i = 0. \quad (2)$$

Since $\sum_j a_{ji} = 1$, then

$$P_i = e_i \left(\sum_j a_{ij} P_j + G_i \right) - f_i P_i. \quad (3)$$

The matrix $[a_{ij}]$ is given in Table 2, and the vectors for e_i and f_i in Table 3. Upper closure is obtained by total removal of fish guilds by fishing and top predators. Marine mammals and seabirds are implicit as top predators in this budget. Estimates of their consumption of fish (Yodzis, 2001) are ~ 4 and 1%, respectively. The coupled set of Equation (3) was solved by matrix inversion to obtain the annual production of each trophic component

Table 4. Maximum and mean fractions of biomass contributed by the annually dominant species within each of the three fish guilds over the 40 years 1963–2002.

Fraction	Piscivores	Benthivores	Planktivores
Maximum	0.71	0.74	0.92
Mean	0.41	0.43	0.59

(Table 3). These results were used as a baseline (Scenario 0) for comparing with production in other scenarios.

Foodweb scenarios

Our goal was to examine the consequences of alterations in particular ecosystem processes on the yields of haddock, a benthivore, and Atlantic cod, a piscivore. To do this, we first estimated changes in the feeding guilds of the fish produced by changes in internal foodweb processes. To translate from guilds to species requires estimates of the maximum, or expected, fraction contributed by member species to the total biomass of each guild. Using the fish biomass data of Steele *et al.* (2007), we calculated the maximum fractional abundance of each guild member for each year, then found the 40-year maximum and mean, as percentages, for all three guilds (Table 4).

A variety of explanations has been invoked for the major changes in the fish communities on Georges Bank and other fishing grounds in the western North Atlantic (Jackson *et al.*, 2001; Beaugrand *et al.*, 2003; Worm and Myers, 2003; Choi *et al.*, 2004; Frank *et al.*, 2005; Myers *et al.*, 2007). We consider a set of scenarios that simulate such changes in the trophic groups resulting from adaptations in internal foodweb processes. These scenarios are produced by altering the relative magnitudes of fluxes in the foodweb from the baseline 1993–2002 production values (Table 3). Technically, this is done by changing values in the production matrix (Table 2; see Appendix for changes). The results are expressed as percentage changes from the baseline values in the production of plankton, benthos, and juvenile fish as prey (Figure 3a) and in the production of planktivores, benthivores, and piscivores as consumers (Figure 3b).

Scenario I: piscivores are the dominant fish guild

We transferred 70% of the production of planktivores and benthivores to the piscivores, while retaining the proportions of juvenile fish, plankton, and benthos in the piscivore diet. This change gave the piscivore guild 66% of total production, matching the maximum in Figure 2a. The result was a 200% increase in piscivore production (Figure 3b). Total fish production is reduced because more food goes through the juvenile fish.

Scenario II: benthivores are the dominant guild

The benthivore diet consists predominantly of benthos, so relatively little food can be reallocated from the other fish guilds, especially planktivores. Switching some benthos production from piscivores to benthivores increases benthivore production by just 111% (Figure 3b).

Scenario III: carnivorous zooplankton are eliminated

There are many suggestions in the recent literature (Pauly *et al.*, 1998; Jackson *et al.*, 2001; Mills, 2001; Lyman *et al.*, 2006) that overfishing has produced a marked increase in gelatinous zooplankton. On Georges Bank, the invertebrate predators on mesozooplankton include ctenophores, chaetognaths, hydroids, and

carnivorous copepods. As an extreme case, we have removed them from the foodweb so that the mesozooplankton production goes directly to fish. This removal increases piscivore production by just 51% (Figure 3b). Understandably, planktivore production also increases, but the benthivore increase is negligible.

Scenario IV: carnivorous benthos is eliminated

Increases in shrimps, crabs, and lobsters in the North Atlantic (Worm and Myers, 2003) and the North Sea (Heath, 2005) have been attributed to overfishing of cod and other demersal species. An increase in crustaceans has not been reported on Georges Bank, but as an extreme case we eliminated all benthic invertebrate carnivores. Elimination of that link results in an increase of only 32% in piscivore production, but 60% in benthivore production (Figure 3b).

Scenario V: production of suspension-feeding benthos is increased

In the analysis of food consumption by fish over the four decades, consumption of benthos as a percentage of total fish intake decreased from >60% at the beginning of the time-series to ~30% in later decades (Figure 2a; Steele *et al.*, 2007). We simulated this process by redirecting the fluxes of phytoplankton from mesozooplankton to suspension-feeding benthos. This reallocation changed the percentage of benthos in the aggregate fish diet from 31 to 65%, close to the observed change. The switch from plankton to benthos also increases the total (plankton plus benthos) food available because the benthos, unlike the plankton, is not subject to fractional loss by physical export off the Bank. This change resulted in a large increase in benthivore production and a much smaller increase in piscivores (Figure 3b).

Scenario VI: the role of microzooplankton is reduced

It is not evident that changes in fish stocks will restructure the lower trophic web, but this type of trophic cascade has been documented for other ecosystems (Frank *et al.*, 2005; Oguz and Gilbert, 2007). To illustrate changes within the lower web, we reduced consumption of phytoplankton by microzooplankton by one-third and redirected it to the suspension-feeding benthos. As expected, the scenario produced a large increase in benthivore production (219%) and smaller gains in piscivores (88%; Figure 3b).

Scenario VII: direct input of phytoplankton to detritus is eliminated

Bacterial decomposition of detritus in recycling nutrients is a critical process, but its magnitude in any system is uncertain. In calculating energy budgets for Georges Bank, Steele *et al.* (2007) took the fraction of detritus recycled to NH_4 as an unknown and used it to match the calculated and observed rates of recycling. To illustrate the possible effects of decreased recycling, we eliminated the direct input of phytoplankton to detritus. Again, the benthivores gained more than the piscivores (Figure 3b).

Scenario conclusions

The general conclusion from these scenarios (Figure 3b) is that, for piscivores, including cod, the main factors increasing production occur at the higher trophic levels by redistributing fish food (Scenario I) or removing pelagic invertebrate predators (Scenario III). For benthivores, including haddock, the primary increases are at lower trophic levels, and they depend largely on the switch from mesozooplankton to suspension-feeding

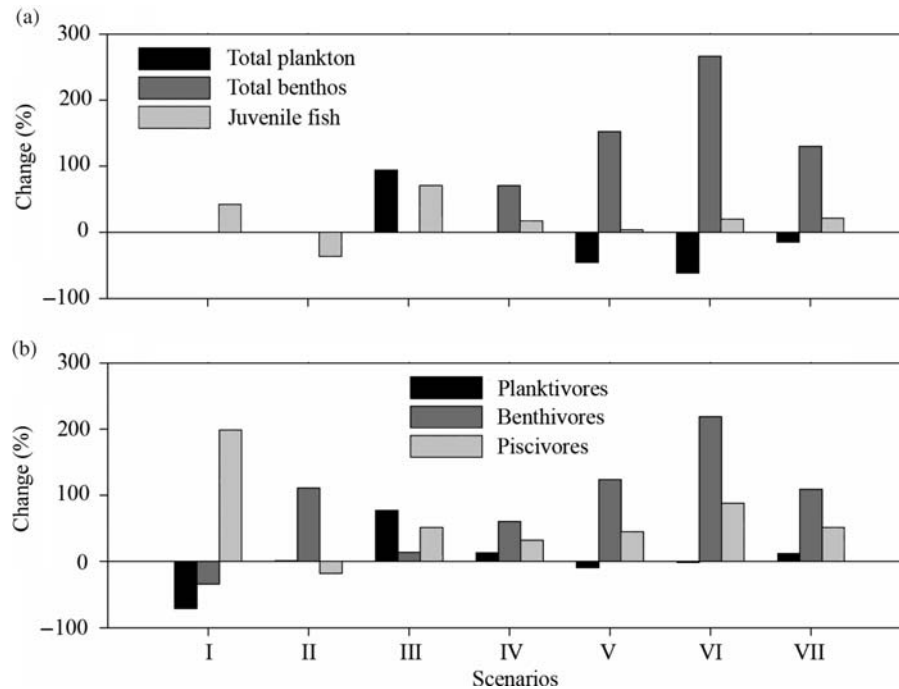


Figure 3. Effects of individual foodweb scenarios, I–VII, on (a) percentage changes in production of total plankton and benthos available as food for fish and of juvenile fish that form part of the diet of piscivores, and (b) the production of the three feeding guilds.

benthos (Scenarios V and VI). The changes produced by Scenario IV are relatively small and, because there is no evidence of increased carnivore populations in the benthos on Georges Bank, we do not consider this scenario further. Similarly, there is no evidence for changes in the lowest trophic levels, so Scenarios VI and VII are not considered further, although they could enhance the switch to benthivores.

Relation to fishery yields

As a prelude to considering future changes, we evaluate how well foodweb Scenarios I–VII explain past fishery yields. Several authors (Pauly, 1995; Kurlansky, 1997; Myers *et al.*, 2007) have pointed out the problems of “shifting baselines” and emphasized the difficulty of reconstructing the pristine structure of ecosystems such as Georges Bank that have been exploited for centuries (Hennemuth and Rockwell, 1987; Steele and Schumacher, 1999). Quantitative data on landings of cod and haddock extend back to the start of the 20th century (Figure 4). The early dominance of cod landings is attributed to the fact that haddock did not salt well (Hennemuth and Rockwell, 1987). From 1921 to 1950, the stocks were not considered to be overfished (Hennemuth and Rockwell, 1987), providing one set of reference values (Figure 5). After the combined period of low basic productivity and excessive fishing effort in the 1960s and early 1970s (Gifford *et al.*, 2009), the relative magnitude of cod and haddock catches was reversed for the two decades 1971–1990 (Figure 5). Finally, for the decade used to construct the foodweb budget, 1993–2002, both fisheries were at a low level (Figure 5). These observations provide a baseline for comparison with the foodweb scenarios (Figure 3).

The values of MSY of cod and haddock in Figure 5 are taken from the most recent available estimates (NEFSC, 2008). To relate haddock and cod production to the scenarios for their

respective guilds, we take 71 and 74% as the maximum percentage production for a single species in the respective guilds (Table 4). To convert the foodweb production rates, P ($\text{gC m}^{-2} \text{ year}^{-1}$), to fishery yields, Y (t year^{-1}), for the whole of Georges Bank, we use

$$Y = \frac{F}{C/B} \times \frac{PA}{P/B} \times \frac{MSY}{B_{MSY}}, \quad (4)$$

where F is the fraction of guild production allocated to cod or haddock (Table 4), A the area of Georges Bank ($43\,000 \text{ km}^2$), C/B the ratio of carbon to biomass (0.114), and P/B the production–biomass ratio of piscivores (0.41) or benthivores (0.39; Steele *et al.*, 2007). We used the most recent estimates of MSY and biomass at MSY (B_{MSY} ; NEFSC, 2008) to calculate the exploitation rate (U_{MSY}) and hence the fraction of production required to support the fishery at MSY (Table 5).

In Figure 5, Scenario 0 represents the maximum potential yields of cod and haddock assuming no change from the 1993–2002 foodweb configuration in terms of fish diets (Table 1), other than realizing maximum dominance of these species within their respective guilds. The yields are intermediate between the earlier (1921–1950) and middle (1971–1990) periods and can almost achieve the MSY levels for haddock and cod if both species are at their maximum achievable abundances within their respective guilds (Table 4). If cod and haddock abundances are closer to the recent 40-year average dominance (Table 4), yields would be well below the MSY estimated. Therefore, it is necessary to consider the consequences of changes within the foodweb.

Scenario I switches the available food towards cod (Figure 5), but the switch does not benefit haddock and requires a massive reduction in pelagic fish (Figure 3b). Another possibility is to reduce significantly the role of invertebrate pelagic predators

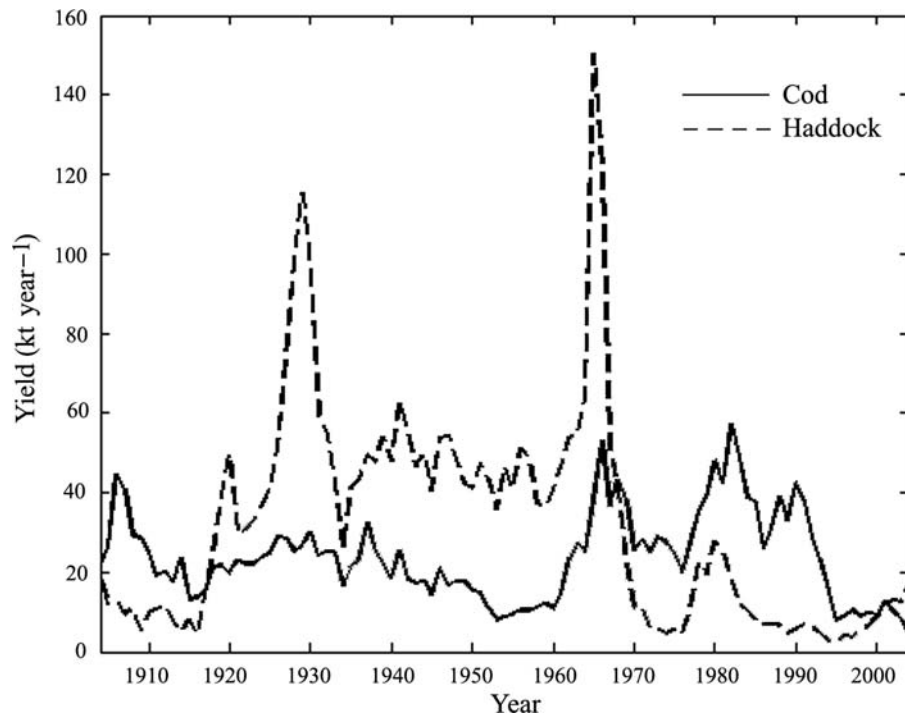


Figure 4. Annual landings of cod and haddock from Georges Bank (from the NOAA website: www.nefsc.noaa.gov/nefsc/publications/).

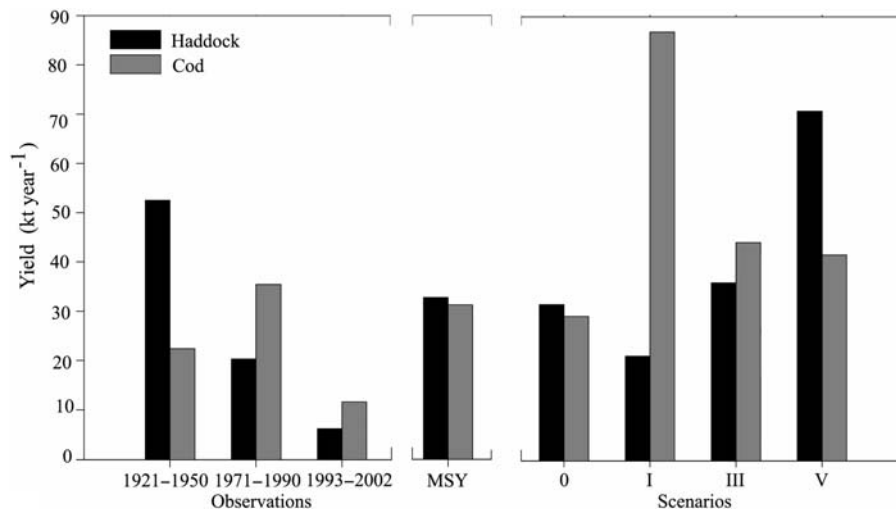


Figure 5. Average biomass yields of haddock and cod for three periods on Georges Bank compared with MSYs and with yields estimated from various foodweb scenarios assuming that cod and haddock yields are 71 and 74% of their respective guilds (see text).

(Scenario III; Figure 5). This scenario increases the abundance of all fish guilds and, in particular, corresponds to the relative abundance of cod and haddock in the period 1971–1990. Although there is increasing speculation about such ecosystem alterations (Jackson *et al.*, 2001; Mills, 2001; Lyman *et al.*, 2006), there is no direct evidence of such a change in the Georges Bank foodweb.

Scenario V involves the redistribution of primary production from mesozooplankton to benthos, particularly epifaunal suspension feeders (Figure 5). This change produces relative abundances of cod and haddock similar to the earlier 1921–1950 period. The overall increase in the production of all fish guilds (Figure 3) arises from the decrease in washout of plankton from Georges Bank

when the benthos is dominant. Washout of plankton from this relatively small offshore fishing ground is more significant than for larger coastal ecosystems (Klein, 1987). This scenario explains the relative abundance of benthic-feeding fish in the decades before 1970, compared with areas such as the North Sea (Cohen and Grosslein, 1987) and with the present Georges Bank ecosystem. Steele *et al.* (2007) showed that the fraction of benthic food in the aggregate fish diet declined from ~ 0.6 in the early 1960s to ~ 0.3 after 1980 (Figure 2c). This shift can be linked to the greatly increased habitat disturbance occasioned by modern trawling methods (Hermsen *et al.*, 2003) and/or to environmental changes (Collie *et al.*, 2008).

Table 5. MSY, biomass at MSY (B_{MSY}), and exploitation rate at MSY (U_{MSY}) for four Georges Bank fish stocks (after NEFSC, 2008).

Species	MSY (t)	B_{MSY} (t)	U_{MSY}
Cod	31 159	148 084	0.210
Haddock	32 746	158 873	0.206
Yellowtail flounder	9 400	43 200	0.218
Winter flounder	3 500	16 000	0.219

Discussion

The use of scenarios in this analysis depends on the acceptance of a linear steady-state description of the Georges Bank trophic web. The natural system is unlikely to be linear, and certainly is not at steady state, even as an annual average. However, non-linear dynamic simulation models with large numbers of state variables are unlikely to be more realistic and have less heuristic value (Oreskes *et al.*, 1994; Ginzburg and Jensen, 2004). Because linear bottom-up simulations of foodwebs are generally donor-controlled (Steele, 2009) and therefore stable, these scenarios represent asymptotic changes in dynamic simulations (Steele, 2009). We have not performed specific sensitivity analyses, but the scenarios approximate the sensitivity of the system to changes in the parameters (Appendix). Given these caveats, four inferences may be drawn from these calculations and from Steele *et al.* (2007), beginning with physical processes at the base of the trophic web.

- (i) Physical forcing, demonstrated by the changes in the decade 1963–1972, can decrease production by a factor of two compared with later decades and must be considered a natural process influencing fish production. Our linear budget model implies that any change in nutrient flux affects the fish guilds equally. Large changes in nutrient supply could affect the partitioning of energy in the lower trophic web, but we have no evidence for a non-linear assumption in continental-shelf ecosystems. It seems unlikely that top-down cascades would alter nitrogen recycling within the microbial web significantly. Possible connections to climatic change (Pershing *et al.*, 2001) suggest a link to periods of negative NAO index. Because the years 1955–1972 experienced the most sustained negative NAO index during the past century (Wisbeck *et al.*, 2001), the total productivity in earlier and later decades may be comparable.
- (ii) Within this overall productivity, a long-term switch from benthic to pelagic production in the 1970s is indicated by a 50% reduction in the fraction of benthos in the aggregate fish diet (Steele *et al.*, 2007). This switch can be attributed to habitat destruction by mobile fishing gear (Hermesen *et al.*, 2003). If nutrient fluxes were comparable for the inter-war period and the decade 1993–2002, then the yields of haddock and cod during the years 1921–1950 would be achieved with 56 and 40% presence in their respective guilds. This is significantly less than the maximum observed value of 72% required with the *status quo* and is closer to the long-term averages (Table 4).
- (iii) In the various scenarios, the largest changes in cod and haddock stocks arise from major restructuring of the fish community that changes the pattern of species dominance within the fish diet guilds. The marked decline of cod after the 1980s was balanced by an outburst of another piscivore,

winter skate, a predator of sand lance (*Ammodytes americanus*; Gifford *et al.*, 2009). The subsequent decline in winter skate corresponded to an increase in other piscivorous species, principally spiny dogfish (*Squalus acanthias*). The decline in haddock corresponds to a reduction in the proportion of benthic food in the aggregate fish diet (Steele *et al.*, 2007), and also with some increase in another benthivore, ocean pout.

- (iv) Possible increases in pelagic and benthic invertebrate predators are frequently proposed as factors that could result in significant diversion of food energy from vertebrates (Jackson *et al.*, 2001; Worm and Myers, 2003). There is no evidence of an empty fish niche on Georges Bank, nor should we expect to find such evidence. Significant increases in one fish guild require decreases in others, or major changes within the foodweb. An increase in cod within the piscivore guild would require decreases in other piscivores—such as the elasmobranchs, winter skate, or spiny dogfish—or changes in other guild species such as haddock, herring, or mackerel, which maintain the overall balance in the diet of plankton, benthos, and juvenile fish.

The present challenge is to rebuild the principal demersal species, including cod and haddock, in an ecosystem with an altered fish species composition. Thanks to a very large 2003 year class, Georges Bank haddock are now considered to be in the process of rebuilding (NEFSC, 2008), but recent low growth rates suggest that production of benthic food may limit the recovery. The yields of other species in the fish community must also be considered. For example, the combined MSY of the benthivores haddock, yellowtail flounder (*Limanda ferruginea*), and winter flounder (*Pseudopleuronectes americanus*) totals 45 600 t (Table 5). Under Scenario 0, the entire production of the benthivore guild would be required to support this combined yield. Scenario III, IV, or V would be required to allow production of the other 11 species in the benthivore guild (Steele *et al.*, 2007). There are several migratory species for which it is difficult to assign a yield to Georges Bank. Of these, Atlantic herring and Atlantic mackerel are at historically high levels of abundance (Steele *et al.*, 2007), a situation that exacerbates the challenge of recovering demersal fish stocks in a pelagic-dominated ecosystem.

In summary, we cannot specify whether past or future mechanisms of change, such as regime shifts (Collie *et al.*, 2004), are responsible for the decline in cod and haddock stocks or are required for their recovery. Our approach cannot define the cause of transitions from one state to another, nor the modifications required to rebuild the demersal fish stocks on Georges Bank. The observed trends in the patterns of dominance within the fish community implicate overfishing as a primary cause of past changes on Georges Bank, and any future increase in commercial stocks will require significant redistribution within the fish community. A return to the balance of species present during the first half of the 20th century will depend, in our opinion, on an increase in the fraction of primary production going to the benthos and may require changes in benthic habitats.

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Appendix

Changes to the percentages in matrix $AP = [a_{ij}]$ (Table 2) required for the seven scenarios.

Scenario I	Scenario II	
$AP(14,12) = 55$	$AP(14,12) = 25$	
$AP(14,13) = 42$	$AP(14,13) = 18$	
$AP(15,12) = 18$	$AP(15,12) = 63$	
$AP(15,13) = 5$	$AP(15,13) = 17$	
$AP(15,14) = 4$	$AP(15,14) = 30$	
$AP(16,12) = 1$	$AP(16,12) = 5$	
$AP(16,13) = 19$	$AP(16,13) = 57$	
$AP(16,14) = 2$	$AP(16,14) = 13$	
$AP(17,12) = 25$	$AP(17,12) = 7$	
$AP(17,13) = 33$	$AP(17,13) = 9$	
$AP(17,14) = 94$	$AP(17,14) = 57$	
Scenario III	Scenario IV	
$AP(5,4) = 0.1$	$AP(9,6) = 0.1$	
$AP(12,4) = 22.9$	$AP(13,6) = 19.9$	
	$AP(9,8) = 0.1$	
	$AP(13,8) = 99.9$	
Scenario V	Scenario VI	Scenario VII
$AP(4,2) = 6$	$AP(3,2) = 40$	$AP(6,3) = 25$
$AP(6,2) = 26$	$AP(4,2) = 6$	$AP(11,3) = 1$
	$AP(6,2) = 46$	$AP(6,2) = 14$
		$AP(11,2) = 0$

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